

**Mass Flowering and Flower Morphology of
Shibataea chinensis Nakai (*Poaceae: Bambusoideae*)
Cultivated in the Fuji Bamboo Garden, Japan**

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(Received on June 30, 2008)

In 2008, a mass flowering of *Shibataea chinensis* Nakai, which is cultivated in the Fuji Bamboo Garden, Japan, was observed. On February 3, a majority of the culms bore young inflorescences on their nodes. On March 23, the inflorescences were in full bloom with green leaves. Flowering terminated around April 20. All the inflorescences withered although the anthers protruded from the apices of withered florets, and did not bear any fruits. Even after flowering, the flowered culms remained verdant with green foliage leaves and bore new leaf buds on the axils. The inflorescence of *S. chinensis* was an indeterminate compound pseudospikelet. It comprised six secondary pseudospikelets, three tertiary pseudospikelets, and three spikelets, where the former two each had one prophyllate bud. A hermaphrodite floret is composed of a lemma, a palea, 3 lodicules with unicellular long hairs and bi- or tri-cellular microhairs on the margin, 3 stamens with 10-mm-long anthers and an ovule with 3 papillose stigmas.

Key words: Indeterminate inflorescence, lodicule, mass flowering, prophyllum, pseudospikelet, *Shibataea chinensis*.

Shibataea chinensis Nakai (1933) was described based on the morphology of its sterile organs such as culms and foliage leaves. Thereafter, there have been no flowering records, although Geng and Wang (1996) have cited the description of Nakai in the Chinese bamboo flora.

In the spring of 2008, a mass flowering of *Shibataea chinensis* occurred in the Fuji Bamboo Garden, Japan. In this study, we reported the flowering process and

flower morphology of *S. chinensis*, and we compared them with the findings of the congeneric species *S. kumasasa* (Zoll.) Makino (Nakai 1933, Takagi 1958, 1960, Suzuki 1978).

Materials and Methods

A *Shibataea chinensis* clump, that is a clone introduced from the Nanjing Forestry University, China, in October 1985, was maintained in the Fuji Bamboo Garden

located at Nagaizumi, Shizuoka Prefecture, Japan. The *S. chinensis* clump was 21 m² and its culm density was approximately 690 culms/m². From this clump, 20 culms were randomly sampled for obtaining the following average measures: culm height, 83 cm; diameter, 2.5 mm; and mid-culm internode, 13.7 cm. On November 9, 2007, we found flower buds on the culm nodes for the first time. Thereafter, we observed the flowering process from February to May 2008.

In each observation, we collected the inflorescences, foliage leaves, and rhizomes, fixed the materials with Farmer's fixative and prepared a stock in absolute ethanol, and then examined their precise morphology under a dissection microscope at 7–20× magnification. Lodicles were observed and photographed using a light microscope equipped with a Nomarski interference optics, OLYMPUS BH2-NIC. The voucher specimens YH & MK 531, 547, and 554 are kept in the herbaria TI and the Department of Forest Science, Utsunomiya University, Japan.

Terminology in the bamboo inflorescence

McClure (1966) has defined many terms to describe various characteristics of bamboo morphology, development, and life history traits. Thus, we adopted McClure's definition on bamboo inflorescences as follows;

Prophyllum A 2-keeled sheathing organ which at first surrounds the branch primodium to form a bud becoming inserted circumaxially at the proximal node of a branch. A palea is a corresponding organ in a spikelet. Prophylla are sometimes called bracts, or bracteoles.

Spikelet A basic structure of gramineous inflorescence, comprising a segmented axis called a rachilla and its appendages. The

appendages beginning with the lowermost are empty glumes, followed by lemmas, and branches of the rachilla bearing a palea and the parts of a flower, which are subtended by each lemma.

Pseudospikelet The pseudospikelet is recognized by the presence of a two-keeled prophyllum at its base, followed by one or more bud-subtending bracts. The axis of a pseudospikelet is the rachis; while the distal part is the rachilla of the spikelet. The transition between the lower part of the pseudospikelet and the spikelet (spikelet proper) that follows is marked by the initiation of the development of abscission layers at the nodes of the axis and often by the intercalation of one or two empty glumes. Primary, secondary, or successive ordered pseudospikelets are correlated with their respective positions on the axis that bears them. The primary pseudospikelet is an originating whole branching system in which the lateral or the terminal pseudospikelets are the secondary, while successive higher ordered ones are borne on them. A lateral pseudospikelet is the sessile type with a two-keeled prophyllum at its base as the first proximal foliar appendage, while a terminal one is made pedicellate by the distal internode with usually an unkeeled bract instead of the two-keeled structure located far below at the base of the branch itself.

Determinate and indeterminate inflorescences

The definition of determinate and indeterminate inflorescences for Graminae by McClure (1966) is quite different from the ordinary and general morphological definition. A determinate inflorescence is defined that where each branch terminates in a conventional spikelet and no meristems remain afterward in the form of dormant lateral bud. While, an



Fig. 1. *Shibataea chinensis*. a. Mass flowered clump. b. Young inflorescences on February 3, 2008. c. Inflorescence in full-bloom with drooping anthers on March 23, 2008. d. Withered inflorescence with protruding anthers (arrows) from apices of the florets on May 3, 2008.

indeterminate inflorescence is defined that where prophyllate buds at the proximal nodes of pseudospikelets bear fresh bodies of meristem and the development of new branches from these buds may be continuous or intermittent and reactivated on a seasonal basis for a period lasting in some cases for several successive years.

Results

Mass flowering process

On February 3, 2008, a clump of *Shibataea chinensis* exhibited a mass flowering. A majority of culms had 3–5 flowering branches per node, each of which

bore 1–3 inflorescences with or without one foliage leaf (Fig. 1a). The culms and foliage leaves were green, except for the leaf portions that had withered due to the harsh winter. The young inflorescences were whitish purple, fusiform, and 17–26 mm in length (Fig. 2b).

On March 23, the inflorescences were in full bloom. Inflorescences grew to 23–36 mm long with drooping anthers from apices of several florets (Fig. 1c). The anthers were 8–11 mm long and bright yellow in color, and their apices were purple due to the accumulation of anthocyanin. The culms and foliage leaves remained green.

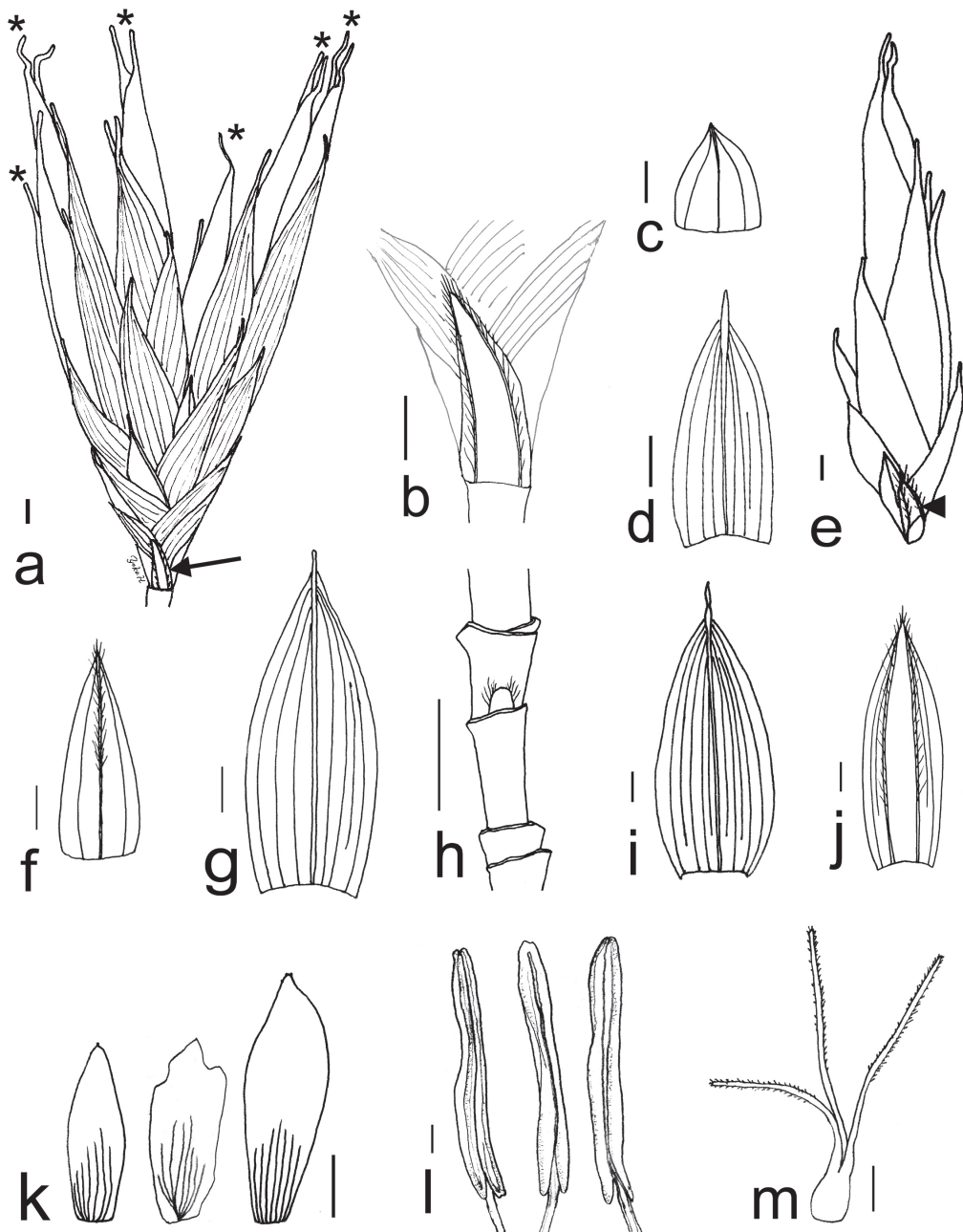


Fig. 2. Floral organs of *Shibataea chinensis*. a. Primary pseudospikelet with a two-keeled prophyllum at its base (arrow) and secondary pseudospikelets (asterisks). b. Close-up of base of (a) to show a two-keeled prophyllum. c. One-keeled bract. d. Lemma-like bract. e. Secondary pseudospikelet with a prophyllum at its base (arrowhead). f. One-keeled empty glume. g. Lemma-like empty glume. h. Prophyllate bud at a node in (e) which is removed bracts and empty glumes. i. Lemma. j. Palea. k. Lodicules. l. Anthers with a part of filament. m. Gynoecium. Scale bars = 1 mm.

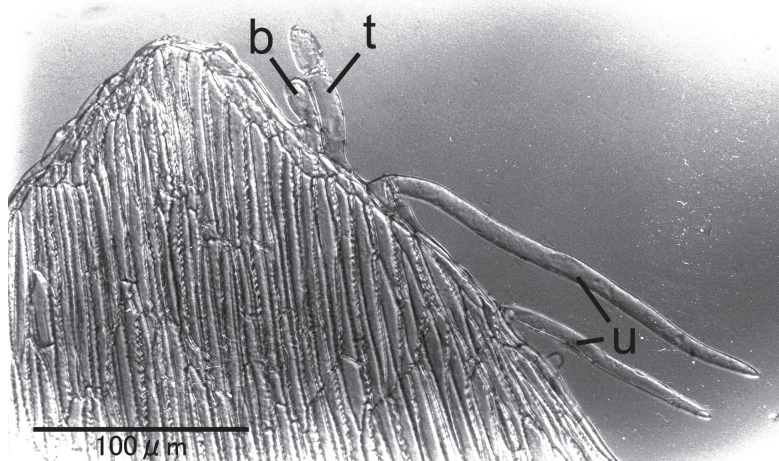


Fig. 3. Micrograph of the uppermost margin of a lodicule shown in Fig. 2j taken with a light microscope equipped with a Nomarski optics. b. Bicellular microhair. t. Tricellular microhair. u. Unicellular long hairs.

Around April 20, the flowering had ceased. On May 3, although the anthers protruded from the apices of florets (Fig. 1d; arrows), all the inflorescences had withered, and did not bear any fruits. The flowered culms remained verdant with green foliage leaves even after flowering. Some flowered culms bore new leaf buds and several new culms emerged from rhizomes.

Inflorescence and flower morphology

An inflorescence of *Shibataea chinensis* was composed of pseudospikelets of multiple orders, called primary, secondary, and tertiary pseudospikelets in the present paper (Fig. 2a). A primary pseudospikelet is characterized by a two-keeled prophyllum borne at the basal-most portion of the inflorescence. The prophyllum of *S. chinensis* is 2–3 mm long with two ciliated keels and borne at the base of the inflorescence (Figs. 2a, arrow; 2b). It is followed by bud-subtending bracts which can be distinguished into two types: one-keeled bract is glabrous and glossy in texture, 3–4 mm in length

and with 2 nerves (Fig. 2c), and another is sharp spined, 4–5 mm in length, with 7–8 nerves, and similar to a lemma (Fig. 2d). A secondary pseudospikelet is fusiform, 18–23 mm long, and has a two-keeled prophyllum at its base (Fig. 2e; arrowhead), followed by empty glumes which can be also distinguished into two types: one is one-keeled type, 4–5 mm in length and with 2 nerves (Fig. 2f), another is lemma-like type, 7–8 mm in length and with 7–8 nerves (Fig. 2g). A prophyllate bud is 0.3–0.4 mm long with cilia and enclosed by the uppermost lemma-like glume (Fig. 2h). In the hermaphroditic floret (Fig. 2i–m), the rachilla segments are 1 mm long. The lemma is acuminate lanceolate, 13–15 mm long with 11–13 nerves (Fig. 2i). Note that the lemma and lemma-like appendages are distinguished from each other by their nerve numbers. The palea is 8–12 mm long with 2 ciliate keels, having 2 nerves on either side (Fig. 2j). Three lodicules are broadly navicular and acute or obtuse, 3–4 mm long and with 7–8 nerves (Fig. 2k). They have a filmy texture on their lower portions.

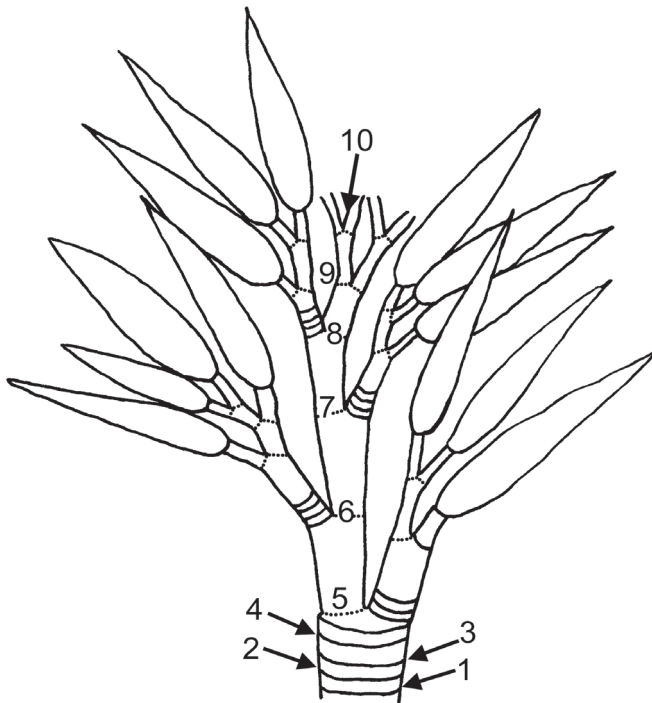


Fig. 4. Diagram of main axis of a primary pseudospikelet of *Shibataea chinensis* shown in Fig 2a. Numbers of 5–10 show each node on main axis from proximal to distal.

There are 3 stamens with 8 to 11-mm-long anthers (Fig. 2l) and 13-mm-long filaments when they are in full bloom. An ovary is ovoid with 3 papillose stigmas (Fig. 2m). A well developed floret has lodicules with unicellular long hairs and bi- or tri-cellular microhairs on the crenulate margin at the uppermost regions (Fig. 3).

Diagrammatic representation of primary pseudospikelet in *Shibataea chinensis*

The compound pseudospikelet illustrated in the Fig. 2a is schematically shown in Fig. 4. The primary pseudospikelet has a two-keeled prophyllum on its base at the first node, followed by one-keeled and lemma-like bracts, and terminates in a spikelet (S1) on a main axis. As shown in Figs. 4 and 5, six secondary pseudospikelets, Ps1 to Ps6,

are alternately developed on the main axis at the axil of each lemma-like bract at nodes 5 through 10, respectively.

We showed schematic and interpretative diagrams of dissected branching system of the primary to tertiary pseudospikelets (Fig. 6). In the primary pseudospikelet, the prophyllate buds at nodes 5 through 10 develop to be the secondary pseudospikelets, and each prophyllate bud in the secondary pseudospikelet develops into the tertiary one. The prophyllate buds on the tertiary pseudospikelets are dormant. As shown in Fig. 5, the Ps1 pseudospikelet bore two tertiary pseudospikelets (Pt1 and Pt2) and terminated in a spikelet (S2). The Ps5 pseudospikelet also had one tertiary pseudospikelet (Pt3) and a spikelet (S3). The secondary and tertiary pseudospikelets

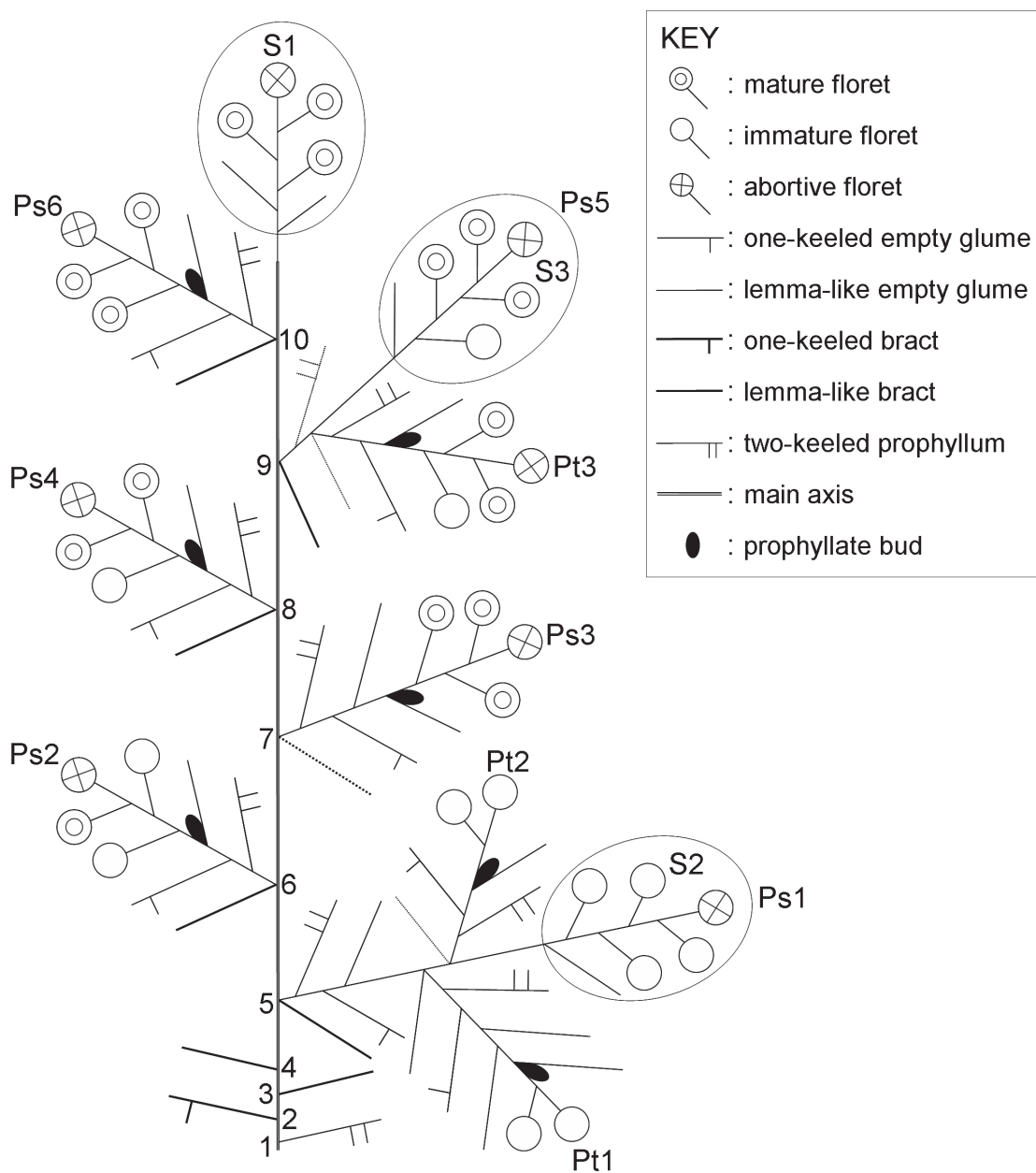


Fig. 5. Schematic and interpretative diagram of the primary pseudospikelet of *Shibataea chinensis*. The primary pseudospikelet consists of six secondary pseudospikelets (Ps1–6), three tertiary pseudospikelets (Pt1–3), and three spikelets (encircled, S1–3). Numbers of 1–10 show each node on main axis corresponding to numbers in Fig. 4. Broken line represents hypothetical missing position of glume, bract, and prophyllum.

bore a two-keeled prophyllum at the base, followed by 2–4 empty glumes. The lowest empty glume is of the one-keeled type, while the others lemma-like type. A prophyllate bud is borne at the node enclosed with the uppermost lemma-like glume. All spikelets, one on the primary pseudospikelet (S1) and other two on the secondary pseudospikelet (S2 and S3), bore no two-keeled prophyllum and 4–5 florets enclosed with 1–2 lemma-like empty glumes. Lateral florets of each secondary and tertiary pseudospikelet are hermaphroditic, and a terminal floret of each pseudospikelet is abortive, except for Pt1 and Pt2.

We added some hypothetical missing positions of glume, bract, or prophyllum because a few deletions of these appendages were always found out at unparticular nodes varying with every sample on primary, secondary, or tertiary pseudospikelets, and to show each related position of the deleted parts (Fig. 5; broken lines).

Discussion

Why do bamboos wait so long to flower? Janzen (1976) reviewed 43 bamboo taxa and 72 flowering events to deduce the predator-satiation hypothesis. Since then, it has generally been cited as the reason why bamboos have the evolutionary trend of monocarpic mass flowering and death. Hisamoto et al. (2005) reported the typical monocarpic mass flowering and death process of *Phyllostachys meyeri* McClure.

However, not all bamboo species exhibit identical flowering behavior. Numata (1962) revealed that *Phyllostachys bambusoides* Siebold & Zucc. exhibited mass flowering and death without bearing any fruit. In the present study, *Shibataea chinensis* exhibited mass flowering but it did not show monocarpic death; instead,

the culms remained verdant with green foliage leaves even after flowering. All the inflorescences of *S. chinensis* withered toward the end of April when the anthers protruded from the apices of each floret, indicating the termination of flowering. At the Mishima climate observatory near the Fuji Bamboo Garden, no late frost was observed in the atmospheric temperatures through the flowering period from March 23 to May 3, thus suggesting that the withering of the inflorescence may have been caused by endogenous factor(s). If any, another possibility should be ascribed to predation by certain insect larvae, though not confirmed (Janzen 1976). The various flowering behaviors mentioned above suggested that the monocarpic mass flowering of bamboos consists of several major components such as flowering, fruiting, and death. Flowering records of congeneric species of *Shibataea kumasasa* was reported in Nakai (1933), Takagi (1958), and Suzuki (1978), yet being no records of caryopsis. Takagi (1960) presented a sketch of caryopsis, which is the only caryopsis record for this taxon, suggesting that the sterility of *S. kumasasa* is common. Our present study also showed the sterility of *S. chinensis*.

The basic characteristics of flower structure are common between both *Shibataea* species. Takagi (1964) described that lodicules of *S. kumasasa* has scanty 0.3 mm long unicellular hairs along the upper margin. Tateoka and Takagi (1967) examined the lodicule epidermis of 288 species of 146 genera in the grass family and described that *Shibataea kumasasa* lodicules has bicellular microhairs. In our results, *S. chinensis* has unicellular long hairs and bi- or tri-cellular microhairs on the crenulated margin at the uppermost region. These facts suggest that *S. chinensis*

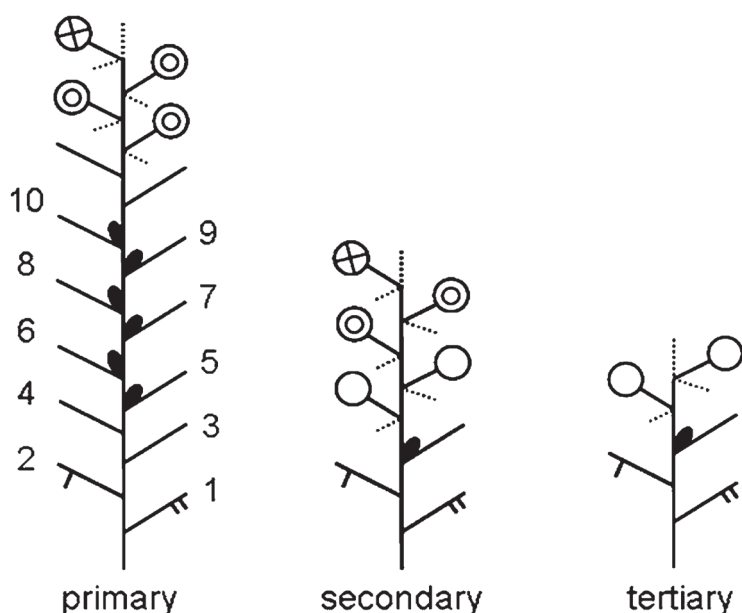


Fig. 6. Schematic and interpretative diagrams of dissected branching systems of the pseudospikelet in Fig. 5. Numbers of 1–10 show each node on main axis corresponding to numbers in Figs. 4 and 5.

has similar characteristics of lodicule to *S. kumasasa*.

As shown in Figs. 2 and 4, the inflorescence of *Shibataea chinensis* was composed of a single primary pseudospikelet, which is recognized by the presence of a two-keeled prophyllum at its base, six secondary pseudospikelets, and three tertiary pseudospikelets. The secondary pseudospikelets bore prophyllate buds at the axil of the uppermost lemma-like glume. McClure (1966) exemplified a panicle of *Sasa veitchii* (Carrière) Rehder as the determinate inflorescence exhibiting a high degree of simplicity, while *Bambusa multiplex* (Lour.) Raeusch., *Guadua angustifolia* Kunth, and *Phyllostachys nidularia* Munro as the indeterminate one based on the presence of prophyllate buds. Wong (1995) explained the pseudospikelets in referring the indeterminate inflorescences of *Gigantochloa rostrata* K. M. Wong.

He also referred that the following genera bear pseudospikelets: *Bambusa*, *Dendrocalamus*, *Dinorchloa*, *Holtumochloa*, *Kinabaluchloa*, *Maculurochloa*, *Melocanna*, *Phyllostachys*, *Schizostachyum*, *Soejatomia*, and *Thyrsostachys*. The present study showed another genus *Shibataea* also has indeterminate inflorescences.

Soderstrom (1981) pointed out that some variability in the number was found in bracts or prophylla as is the quantity of pseudospikelets ultimately produced, comparing the pseudospikelet structure among *Streptochaeta angustifolia*, *Bambusa atra*, and other bamboos. He explained how the spicate inflorescence of *Streptochaeta* is derived from a theoretical complete type of pseudospikelet by loss of the subtending bracts, prophylla, and some of the buds. Thus, he suggested that the usual spikelet of determinate inflorescence evolved from the pseudospikelet architecture. In this

context, the missing subtending bracts, prophylla, or buds in the pseudospikelet of *Shibataea chinensis* is not considered as the spontaneous one but an evolutionary trait in this taxon.

We greatly appreciate anonymous reviewers for the critical comments and invaluable suggestion. This work was partly supported by a Grant-in-Aid for Exploratory Research No. 18658062 from the Ministry of Education, Culture, Sports, Science and Technology and the Specific Research Assistance B from the Asahi Glass Foundation. Y. Hisamoto was supported by a Grant-in-Aid for JSPS Fellows (20.7324).

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久本洋子^{a,b}, 柏木治次^c, 小林幹夫^{a,b}: 富士竹類植物園に植栽されたトウオカメザサ (イネ科タケ亜科) の一斉開花と花の形態

2008年2月から5月にかけて, 富士竹類植物園 (静岡県長泉町) に植栽されたトウオカメザサ (別名ガモウチク) *Shibataea chinensis* が一斉開花を起こした. これまで本種における花の形態は報告されていないので, 一斉開花の経過とともに花序および花の外部形態に関する詳細な記載を行った. トウオカメザサの花期は雄しべ抽出途中に花序のみが枯れて終了し, 稈は生存し, 不稔に終わった. 花序は無限花序で, 擬小

穂が数次に分枝した「複擬小穂」を形成する. 一次擬小穂は, 2 竜骨の前出葉に抱かれた芽から発生し, ごく短い主軸に 6 個の二次擬小穂を交互に形成する. また, 各擬小穂の最上位の苞穎に包まれた節に芽を有した. 花器官において, 鱗被の上端縁に単細胞性の長毛と二あるいは三細胞性の微毛が存在し, オカメザサと同等の特徴を持つことが確認された.

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